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THE FORMATION OF INTUMESCENCES ON POTATO PLANTS¹

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(WITH NINE FIGURES)

During the winter of 1904-5, in some experiments to determine the relation of a soil fungus to potato plants, Professor Atkinson planted some potatoes in pots, and after the young shoots were well started they were covered with bell jars to produce a moist atmosphere, which would be more favorable for the growth of the fungus. In a few days intumescences were formed in great numbers, so that a large part of the plant was literally covered with them. This suggested that the potato plant would be an excellent subject with which to experiment to determine the cause of the formation of these intumescences, at least under certain conditions. The matter was then placed in my hands for this purpose. The subject was the more interesting because of the difference of opinion among plant physiologists as to the influence of light stimulus in the formation of intumescences upon plants, as pointed out by Von Schrenk (Q) in his paper on "Intumescences formed as the result of chemical stimulation."

The methods used in the experiments for producing the intumescences were in general as follows: young plants were covered with bell jars and their roots supplied every day with an abundance of warm water, except in those experiments where the roots were kept cold. The absorption of water was thus very great, while the saturated air under the bell jar greatly checked the transpiration.

¹ Contribution No. 115 from the Department of Botany of Cornell University.

For the purpose of experiment, the light and temperature conditions could be easily changed.

The intumescences were formed very quickly, generally within two to five days after covering the plants. Usually they appeared on the upper side of the leaf, but were observed also, in cases where they were very abundant, on the under side and scattered profusely over the upper part of the stem. They did not form on the very young growing leaves at the tip of the stem and rarely on the two mature lower leaves of the shoot. The appearance of these intumescences was very similar to that described by Von Schrenk (9) on the cauliflower. To the naked eye they first appeared as very small greenish-yellow dots, projecting slightly from the surface of the leaf. These rapidly developed in size, became lighter vellow, hemispherical, smooth, and glossy. After about twenty-four hours they became whitish and roughened, and projected prominently from the surface. Usually the central part of the intumescence was slightly yellowish in color, with a ring of more whitish cells around the outside. When they first appeared, the intumescences came out over or near the main veins; but when very numerous, they broke out all over the surface of the leaf and looked very much like incrustations of some crystalline salt. The affected leaves curled over toward the under side, and this curling became the stronger the more intumescences were produced. The single intumescences were from 2 to 3mm in diameter. When formed numerously, however, the single intumescences often became confluent, making large rough patches. These intumescences lasted but a short time; in a day or two they had collapsed and become dry and blackened. A cross-section through the leaf showed that the intumescences were due to the hypertrophy of the cells lying underneath the epidermis. The swollen cells were first found in the palisade layer; they elongated and pushed against the epidermis; and in most of the cells crosswalls were formed. These cells continued to enlarge until the pressure upon the epidermis caused it to break and the palisade cells to push up through. As the cells enlarged, the chlorophyll granules lost their green color, became yellowish, and disappeared entirely from the cells or remained very much reduced, scattered through the bottom parts.

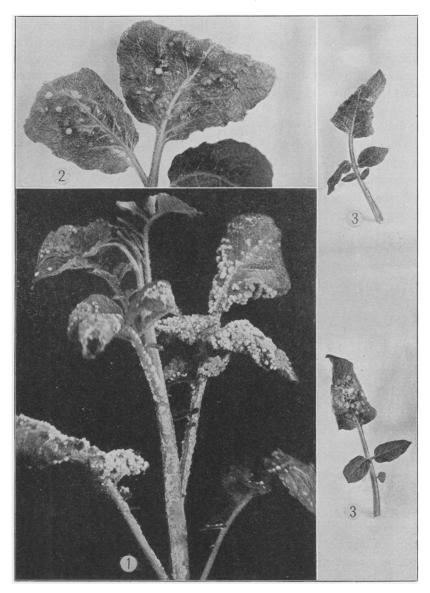


Fig. 1.—Photograph showing intumescences formed on a young potato shoot under whitewashed glass. Figs. 2, 3.—Intumescences formed on a leaf in sunlight.

After the elongated palisade cells had broken through the epidermis, the pressure against their side walls being thus somewhat relieved, the sac-like cells bulged out laterally and became clubshaped at the tip. The central cells stood up perpendicularly to the surface of the leaf, but the cells around the edge of the intumescences curled over toward the leaf surface, thus causing the outside whitish

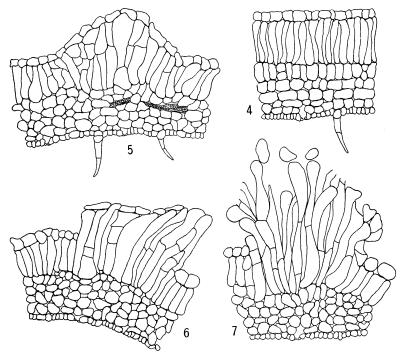


Fig. 4.—Cross-section through a normal potato leaf. Fig. 5.—Cross-section through a young intumescence, showing hypertrophy of palisade layer and formation of cross-walls. Fig. 6.—Later stage; the swollen cells have broken through the epidermis. Fig. 7.—Later stage; some of the cells were cut through in sectioning.

ring of the intumescence, mentioned before. The hypertrophied cells were not confined to the palisade layer, but often included cells in the layer of spongy parenchyma below. In the largest intumescences the swollen cells extended back to one or two rows from the under epidermis. As the intumescences grew old their walls became cutinized.

Intumescences have been observed on various plants by several writers, and all practically agree that they are formed under conditions of excessive humidity accompanied by great warmth. As to

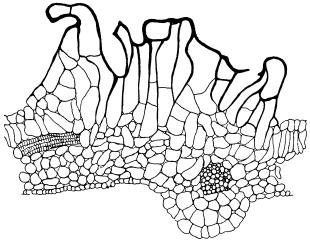


Fig. 8.—Old intumescence; parts of the cells have broken away and the walls have become cutinized.

the presence or absence of a light stimulus, there is a greater difference of opinion. Sorauer (10-20), who has described the majority

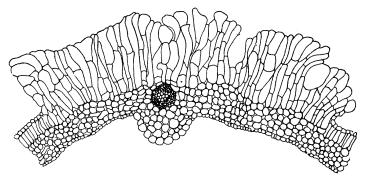


Fig. 9.—Large intumescence or patch formed by the union of several intumescences.

of cases, regards the lack of sufficient light to carry on rapid metabolism as an important factor in their formation. In "Die symptomische Bedeutung der Intumescenzen" (12), in which a number of cases

are described, he finds in every case, except one which developed under forced conditions in the greenhouse, that the intumescences were formed in the fall or winter, when the plants were in their rest period or approaching it. On account of the weak illumination during this time, the plants could not assimilate new building material and thus answered the stimulus of an over-abundant absorption of water by the formation of intumescences.

ATKINSON (I) explains the tomato oedema in a similar way. He says: "With the comparatively small amount of light carbon assimilation is lessened, so that the plant, under the forced conditions of growth, when it needs large quantities of carbohydrates, has to do with a really less quantity than is supplied in the open, when conditions for rapid growth are not so favorable and those for assimilation are improved."

KÜSTER (5) produced artificial intumescences on poplar leaves both in the dark and in the light, but found that when formed in intense light they occurred on the surface of the leaf which lay next the water. He suggested that in this case they did not form on the upper side on account of a more rapid transpiration, due to the strong light.

PRILLIEUX (8) observing the disease on pinks and NOACK (7) on grapes found that intumescences were produced only in weak light.

On the other hand, Dale (3) found that intumescences were not easily produced on *Hibiscus vitifolius* in poor light; were not formed under blue or green glass; but develop readily under red, yellow, or whitewashed glass and in bright light.

VIALA and PACOTTET (21) also strongly emphasize the fact that intumescences are only found in quantity on grape leaves directly under the glass, during periods of most brilliant illumination. These they regard as an effort of the plant to protect the leaf from "chlorovaporization and excessive transpiration" by the formation of a false palisade layer.

According to Von Schrenk (9), intumescences are formed in the Missouri Botanical Garden only under these last-named conditions.

It is a matter of considerable interest, therefore, to determine the conditions under which intumescences are formed in the potato plant.

On March 12, 1906, thirty-six pots of potatoes were planted in

the greenhouse, to be used for the purpose of experiment. Eighteen of the potatoes were planted whole, while in the other pots were placed pieces containing two or three eyes. All of the potatoes were of good size and healthy. By April 4 several shoots had come up some distance from the ground and were covered with the bell jars.

EXPERIMENT I

Four pots of young plants with a few rather small young leaves were placed under bell jars in a well-lighted position in the greenhouse. The temperature of the air within the jars at the time of the setting-up of the experiment was 88° F. For three or four days after it was damp and cold, with only intermittent periods of sunshine. The temperature within the jars averaged about 65° F. In five to six days, after the temperature had increased to 68° F., intumescences began to appear.

Pot 1. Three shoots (from a cut potato), 205,172,128^{mm} high respectively; all had rather small leaves.

Pot 2. Two shoots (from a cut potato), both 62mm high, with young leaves.

Pot 3. One shoot (from a whole potato), 36mm high, with young leaves.

Pot 4. Two shoots (from a whole potato), 32 and 61^{mm} high, with small leaves.

Results

No. 1. After six days intumescences began to appear on all three plants and to assume the characteristic appearance. They were scattered over most of the leaves of the plant and were very numerous on two or three of them. Four days later they had become dry and blackened, but in two days more new ones had appeared.

No. 2. In five days intumescences had appeared on both shoots, although they were rather few and scattered over various leaves.

No. 3. In five days intumescences had formed, but not profusely.

No. 4. In five days a few intumescences had formed.

Intumescences were thus formed upon all of the shoots, but were more numerous on the shoots of pot r. This was probably due to the fact that these plants were farther developed than the others and consequently did not grow so fast. The other plants were very young and grew rapidly, and in consequence made use of more water in growth than the other shoots. A discussion of the connection between growth and the formation of intumescences will be taken up later in this paper.

EXPERIMENT II

At the same time as the preceding experiment, four plants were placed in darkness. The other conditions of temperature and moisture were the same. The bell jars were covered with black cloth to exclude the light.

- Pot 5. One shoot (from a cut potato), 133mm high, with small leaves.
- Pot 6. Two shoots (from a cut potato), 80 and 100mm high, with small leaves.
- Pot 7. Three shoots (from a whole potato), 84, 63, and $25^{\rm mm}$ high, with small leaves.
- Pot 8. Two shoots (from a whole potato), 63 and $25^{\rm mm}$ high, with small leaves.

Results

- No. 5. In darkness eleven days and no intumescences formed.
- No. 6. In darkness eleven days and no intumescences.
- No. 7. In darkness eleven days; in six days two or three intumescences were found on one leaf.
 - No. 8. In darkness eleven days and no intumescences.

These plants were all small and their stems grew very rapidly in the dark. In the three cases where intumescences were not produced, it was thought that this might be due to the rapidity of growth. Accordingly a more developed plant was chosen and placed under the same conditions.

Pot 9. Two shoots (from a whole potato), 105 and 120^{mm} high, with large, well-developed leaves. In two days a few intumescences had formed upon one of the shoots.

It will thus be noted that on two of the plants placed in darkness a few intumescences were formed. It was suggested that this might possibly be due to the fact that the bell jars were not absolutely light tight. Accordingly another pot was placed under the same conditions and the bell jar covered with several thicknesses of cloth to prevent light from filtering through the folds.

Pot 10. Two shoots (from a whole potato), 180 and 96^{mm} high, with large leaves. No intumescences were formed.

These plants, after having been taken from darkness, were left in the light and allowed to develop their leaves. They were then covered with bell jars in the light and after eight days all the shoots, excepting those of pot 10, had developed intumescences.

EXPERIMENT III

The next question which arose was in regard to the effect of increasing the absorption of water by the roots. Pots were placed over the warm water pipes, keeping the soil at a temperature of 70° F. The position of the plant was under whitewashed glass in the greenhouse.

Pot 11. One shoot (from a whole potato), 60^{mm} high, with many large leaves. Pot 12. Two shoots (from a whole potato), 65 and 60^{mm} high, with many large leaves.

Results

No. 11. After four days many intumescences were produced on many leaves. No. 12. After four days intumescences formed on nearly all the leaves and were very numerous on some of them. These intumescences continued to appear for several days.

EXPERIMENT IV

Two plants were kept under the same conditions as in the preceding experiment, with the exception of being darkened by covering their bell jars with black cloth.

Pot 13. Two shoots (from a whole potato), 102 and 62^{mm} high, with small leaves.

Pot 14. Two shoots (from a whole potato), 185 and 130^{mm} high, with large leaves.

No intumescences were formed after ten days on either plant; the growth, however, in both cases was very rapid.

EXPERIMENT V

The absorption of water was lessened by keeping the roots cold. Ice was kept packed around the pots, making an average temperature of the soil about 58° F. The pots were cut off from the air above in the bell jar by a thick blotting-paper covering. The air in the bell jars was kept warm by the sun (about 78° F.) during the days while the experiment was going on. A saturated atmosphere was produced within the jars by the evaporation from dishes of water.

In light

Pot. 15. Two shoots (from a cut potato), 120 and 105^{mm} high, with large leaves.

Pot 16. One shoot (from a cut potato), 190mm high, with large leaves.

In darkness

Pot 17. One shoot (from a cut potato), 130mm high, with large leaves.

Pot 18. Two shoots (from a cut potato), 105 and 150mm high, with large leaves.

Although the plants were kept under these conditions for ten days, no intumescences were formed. The leaves on the plants in the dark became yellow and the plants finally died.

EXPERIMENT VI

Four pots of plants were placed in a shaded portion of the greenhouse over warm water pipes, where their roots would be kept warm.

Pot 19. Two shoots (from a whole potato), 177 and 187^{mm} high, with large leaves.

Pot 20. Two shoots (from a whole potato), 150 and 170 $^{\rm mm}$ high, with large leaves.

Pot 21. One shoot (from a cut potato), 85mm high, with rather small leaves.

Pot 22. One shoot (from a cut potato), 105^{mm} high, with rather small leaves.

Results

In four days the leaves of nos. 19 and 20 were nearly covered with intumescences. Pots 21 and 22 also produced them, but they were not as numerous as on the preceding, and the growth of the plants was more rapid.

From this set of experiments it appears that intumescences appear in light and in the shade when the plants are abundantly supplied with water and their transpiration is reduced. They are found still more abundantly when their roots are kept warmer. Intumescences are not formed in complete darkness nor in light or darkness when the absorption of the roots is lessened by cold. Intumescences were not produced in any case on plants which were not covered by the bell jars.

At the end of this series of experiments all the plants used, as well as those grown outside the bell jars, were cut down and allowed to grow up again. Healthy shoots came up from all the plants excepting those which had been kept in darkness and had been killed by the rotting of their leaves and stems. In about ten days a few of the plants had reached a sufficient height to cover with the bell jars and the preceding experiments were repeated.

EXPERIMENT VII

Plants placed in sunlight and covered May 7.

Pot 23. Two shoots (from a cut potato), 140 and 120mm high, with large leaves

Pot 24. Three shoots (from a whole potato), 150, 170, 180mm high, with large leaves.

In five days both plants showed many intumescences scattered over the leaves. No. 23 was particularly badly affected. There was a cold spell May 7–12, with temperature ranging from 62°-68° F., and a cloudy sky most of the time. On May 12 it became bright and warm, with a temperature of 72° F. Intumescences were then formed in great numbers.

EXPERIMENT VIII

Two plants were placed in darkness at the same time, with the other conditions similar to those of the preceding experiment.

Pot 25. Two shoots (from a cut potato), 180^{mm} with large leaves, and 70^{mm} with small leaves.

Pot 26. Three shoots (from a whole potato), 240, 170, 170^{mm}, with large leaves.

In five days no intumescences were formed and the leaves became yellow and decayed.

EXPERIMENT IX

Two plants were placed under whitewashed glass, with their roots kept warm.

Pot 27. Two shoots (from a cut potato), 150 and 150^{mm} high, with large leaves.

Pot 28. Two shoots (from a cut potato), 200 and 220mm high, with large leaves.

These were covered with bell jars on May 12, a bright warm day with temperature 72° F. In two days intumescences had formed very numerously on both plants. Plant no. 27, as shown in the photograph ($fig.\ 1$), was very heavily covered with intumescences, both on leaves and stem.

EXPERIMENT X

Two plants were placed in the dark, with their roots kept warm.

Pot 29. Two shoots (from a whole potato), 170 and 220 $^{\rm mm}$ high, with large leaves.

Pot 30. Two shoots (from a cut potato), 160 and 200^{mm} high, with large leaves.

No intumescences were formed from May 12 to 15, but the leaves became yellow and decayed.

EXPERIMENT XI

Two plants were kept with their roots cold by packing the pots in ice.

Pot 31. In light; two shoots (from a whole potato), 200 and 190 $^{\rm mm}$ high, with large leaves.

Pot 32. In darkness; three shoots (from a whole potato), 150, 150, 150 mm high, with large leaves.

These plants were left under these conditions from May 15 to 24, and no intumescences were formed. The temperature of the air in the bell jars was about 73° F., and of the soil 55° F.

EXPERIMENT XII

Four plants were placed in the shade, with their roots kept cold. The temperature of the roots averaged 56° F., and of the air above 73° F.

Pot 33. One shoot (from a cut potato), 135^{mm} high, with rather large leaves.

Pot 34. One shoot (from a cut potato), 100mm high, with large leaves.

Pot 35. Three shoots (from a whole potato), 135, 100, 115^{mm} high, with large leaves.

Pot 36. Two shoots (from a cut potato), 210 and 160^{mm} high, with large leaves.

These plants were allowed to remain eleven days under these conditions and no intumescences were formed. Some of the leaves became yellow.

EXPERIMENT XIII

Four plants were placed in the shade, with their roots kept warm from the warm water pipes. The temperature of the air in the bell jars averaged about 84° F.

Pot 37. One shoot (from a whole potato), 170mm high, with large leaves.

Pot 38. Two shoots (from a cut potato), 120 and 100mm high, with large leaves.

Pot 39. Two shoots (from a cut potato), both 130mm high, with large leaves.

Pot 40. Three shoots (from a cut potato), 175, 150, 100mm high, with large eaves.

In four to five days intumescences had formed in very great numbers over all four of these plants.

On May 25, shoots which had come up a third time from the same lot of potatoes were covered with bell jars.

EXPERIMENT XIV

Two pots were placed in sunlight.

Pot 41. One shoot, 150mm high, with large leaves.

Pot 42. One shoot, 200mm high, with a slender stalk and small leaves.

In seven days no intumescences were formed.

EXPERIMENT XV

Two pots were placed in the dark.

Pot 43. Two shoots, 200 and 230mm high, with large leaves.

Pot 44. Two shoots, 300 and 300^{mm} high, with small leaves.

In seven days no intumescences were formed.

EXPERIMENT XVI

Two plants were placed in the shade.

Pot 45. Three shoots, 200, 180, 160mm high, with small leaves.

Pot 46. Two shoots, 200 and 220^{mm} high, with small leaves and a slender stalk.

In seven days no intumescences were formed.

EXPERIMENT XVII

Two plants were placed under whitewashed glass and their roots kept warm.

Pot 47. Two shoots, 240 and 100^{mm} high, with small leaves, but having flower buds.

Pot 48. Three shoots, 60, 150, and 200^{mm} high, with small stalks and leaves. In seven days no intumescences had formed.

That the intumescences did not form at all in this last series of experiments affords a suggestion as to their cause in the first set of young plants. The high osmotic pressure in the cells of the leaf is very probably brought about by the glucose in the leaves, which is furnished in great abundance to the young growing parts from the starch in the tuber, and is also assimilated in light by the leaves. In the case of these last experiments, the shoots which had been sent up the third time from the same tubers would thus be poorly supplied with glucose and the osmotic tension in the cells would not be so great. Sorauer (20), in a recent paper on the formation of internal intumescences on Cereus nycticalis, found a great abundance of glucose in the affected tissue and considered this to be the osmotically active substance which produced abnormal enlargement of the cells when a great amount of moisture was supplied. In the tomato ATKINSON (I) suggested that this substance is some organic acid, the production of which is increased by the low temperature and lessened light conditions under which the oedema developed. It is therefore very probable that the intumescences in the young potato shoots are due to the presence of glucose when the other conditions of a humid atmosphere and an abundance of water for absorption are present.

As before stated, intumescences were not formed in complete darkness, but were developed in very great numbers in the shade and in the light, when supplied with an abundance of water and the root conditions were favorable for absorption. They were not formed on the young growing tips or on the old leaves which had ceased to grow. The explanation would therefore seem to be connected with the phenomenon of growth. It is probable that they did not form in total darkness because here the plants were stimulated to a rapid elongation of the cells in the stem and could thus take care of the abundant water supplied. At the same time, the glucose would not be so abundant as in plants growing in the light, since no assimilation takes place in darkness. For the same reason they did not form on the growing tips of the plants. They were formed in the sunlight and in the shade because elongation of the cells is not so rapid as in the dark and carbon assimilation is active. The plants could not thus take care of the water supplied fast enough, and the abundance of glucose in the growing leaves brought about the abnormal turgescence which caused the intumescences. That the intumescences were not found on the old mature leaves was probably due to the fact that these leaves had stopped growing and the cell walls were firmer, while less glucose was supplied to the cells from the tubers. When the tubers were healthy, intumescences formed equally well on plants from whole and cut potatoes. It would seem, therefore, that bright light is not necessary to the formation of intumescences in the case of the potato plant, nor does it act as a stimulus to their formation. This stimulus comes from the increased absorption of water and lessened transpiration with an abundance of glucose, and when enough light is present to produce the conditions for normal growth and assimilative activity.

To obtain a more accurate knowledge of the light intensity, in the various places in the greenhouse where the plants were placed, Wynn's photographic exposure meter was used. This instrument is manufactured for the use of photographers in measuring light intensity. The light values are obtained by exposing sensitized paper for a

time sufficient to bring it to the shade of a painted standard. The time which is necessary to produce the given shade may then be compared with the time taken to make the standard, which in this case was two to three seconds in bright sunlight at noon. In these experiments four seconds were necessary to produce the standard shade directly under the glass in sunlight, fifteen seconds under the whitewashed glass, and forty seconds in the shade. If the light value of the standard is represented by 1, the proportional light values under the three conditions given would be as follows:

Sunlight	Shade	Whitewashed glass
1.33	13.33	5.00

This method of obtaining light values is described by CLEMENTS (2, pp. 49-64). In order to test the power of new shoots from fresh potatoes to form intumescences, a new set of thirty-six potatoes was planted June 5; and June 25 the shoots were covered by the bell jars.

EXPERIMENT XVIII

In sunlight with an average temperature of 79° F.

Pot 48. Three shoots (from a whole potato), 240, 150, 150 $^{\rm mm}$ high, with large leaves.

Pot 49. Four shoots (from a cut potato), 320, 340, 300, 280^{mm} high, with large leaves.

Pot 50. Three shoots (from a whole potato), with large leaves, 280, 230, $^{\rm 230^{mm}}$ high.

Pot 5τ . Two shoots (from a whole potato), 200 and 240^{mm} high, with large leaves.

Pot 52. Four shoots (from a whole potato), 200, 240, 200, 220 $^{\rm mm}$ high, with large leaves.

After two days intumescences had begun to form, and in three days they had formed on all the plants excepting no. 52. Although this was left covered for a few days longer, intumescences did not form.

EXPERIMENT XIX

Five plants were placed in the shade, with an average temperature of 73° F.

Pot 53. Four shoots (from a cut potato), 240, 280, 210, 260 $^{\rm mm}$ high, with large leaves.

Pot 54. Three shoots (from a whole potato), 260, 230, 270 $^{\rm mm}$ high, with large leaves.

Pot 55. Three shoots (from a whole potato), 120, 130, 150 $^{\rm mm}$ high, with large leaves.

Pot 56. Four shoots (from a whole potato), 250, 240, 220, 100^{mm} high, with large leaves.

Pot 57. Four shoots (from a whole potato), 130, 160, 170, 190^{mm} high, with large leaves.

In two days intumescences had begun to form on all the plants. In three days they were very numerous over all the plants.

EXPERIMENT XX

Five plants were placed in darkness, with an average temperature of 79° F.

Pot 58. Four shoots (from a cut potato), 300, 250, 250, 270 $^{\mathrm{mm}}$ high, with large leaves.

Pot 59. Three shoots (from a cut potato), 280, 300, 290^{mm} high, with large leaves.

Pot 60. Three shoots (from a whole potato), 300, 250, 140 $^{\rm mm}$ high, with large leaves.

Pot 61. Three shoots (from a cut potato), 230, 130, 150^{mm} high, with large leaves.

Pot 62. Three shoots (from a cut potato), 240, 220, 200^{mm} high, with large leaves.

In five days none of the plants had developed intumescences, but they were very badly decayed from the excessive warmth and moisture.

EXPERIMENT XXI

At the same time some of the old plants, the second and third shoots from potatoes planted previously, were placed under bell jars. They all had rather small leaves and slender stems and were from 200 to 300^{mm} high. Three were placed in the shade and three in the sunlight and all failed to produce intumescences.

EXPERIMENT XXII

A few shoots of potatoes were stimulated with the various copper salts used by Von Schrenk (9) in producing this disease on the cauliflower, to see if they would have a like effect upon the potato plant. The leaves of two shoots were stimulated with the following salts: copper ammonium carbonate, copper sulfate, copper acetate, copper nitrate, copper chlorid.

At the same time two shoots of the old plants were stimulated with each of these salts. All of these plants were left uncovered. After twenty-four hours burnt patches appeared on all the shoots wherever the sprays struck. The entire tissue through the leaf to

the under side in these patches was killed. No intumescences were formed on the old plants. On the new plants in two days a few intumescences formed as follows. On the first shoot sprayed with copper nitrate a few intumescences were produced over the veins. On the second shoot a few were formed on the surface. On one shoot sprayed with copper ammonium carbonate a few intumescences appeared at the tip of a leaf. The potato plants which were used, however, were not very healthy ones and developed from poor, shriveled, small tubers. These shoots would not form intumescences under bell jars when supplied with water, which fact was probably due to the leaves being poorly supplied with glucose. Had healthy young plants been used, it is very possible that intumescences would have been readily produced.

SUMMARY

Intumescences are produced on young potato plants from good tubers, when transpiration is checked and the roots are absorbing water. Their formation is increased by conditions which favor an increased absorption of water, as a warm soil, and is prevented by the opposite condition of a cold soil.

Intumescences are formed abundantly both in bright light and in weak light, which shows that light acts as a stimulus to their production only so far as it provides for the normal metabolism of the shoots and leaves.

Intumescences are not produced in total darkness, as this condition favors the rapid elongation of cells in the stem, which can thus make use of an increased supply of water. At the same time there is less of the osmotically active substance present in the leaves in darkness as photosynthesis is not taking place.

The abnormal state of turgescence of the hypertrophied cells is probably due to the osmotic action of glucose, assimilated in part by the leaf, but principally supplied to it from the underground tuber, so richly provided with starch.

In conclusion, I wish to acknowledge the many helpful suggestions of Professor Atkinson, under whose direction this work was undertaken.

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